Mobergellans were one of the first Cambrian skeletal groups to be recognized yet have long remained one of the most problematic in terms of biological function and affinity. Characterized by a disc-shaped, phosphatic sclerite the most distinctive character of the group is a prominent set of internal scars, interpreted as representing sites of former muscle attachment. Predominantly based on muscle scar distribution, mobergellans have been compared to brachiopods, bivalves and monoplacophorans, however a recurring theory that the sclerites acted as an operculum remains untested. Rather than correlate the number of muscle scars between taxa, here we focus on the percentage of the inner surface shell area that the scars constitute. We investigate two mobergellan species, *Mobergella holsti* and *Discinella micans* and compare the Cambrian taxa with the muscle scars of a variety of extant and fossil marine invertebrate taxa to test if the mobergellan muscle attachment area is compatible with an interpretation as operculum. The only skeletal elements in our study with a comparable muscle attachment percentage are gastropod opercula. Complemented with additional morphological information, our analysis supports the theory that mobergellan sclerites acted as an operculum presumably from a tube-living organism. The paucity of tubes co-occurring with mobergellan sclerites could be explained by the transportation and sorting of detached opercula while the corresponding tube remained attached to substrata in shallower water. The opercula perhaps performed a similar role to that seen in serpulid annelids and in neritid gastropods sealing the living chamber of the organism to avoid desiccation or for protection.

ADDITIONAL KEYWORDS Annelida –Brachiopoda – Cambrian – *Discinella* – Gastropoda – Mollusca – Operculum – *Mobergella*

INTRODUCTION

Early Cambrian skeletal fossil assemblages are dominated by a sundry of small tubes, shells, plates and spines that represent some of the earliest representatives of animal groups with mineralized hard parts. Some of these fossils represent the shells of complete microscopic organisms, but others represent elements (sclerites) of larger composite exoskeletons (scleritomes) that are disarticulated post-mortem (Bengtson *et al.*, 1990; Skovsted, 2006; Vannier *et al.*, 2007; Topper *et al.*, 2009; Caron *et al.*, 2013; Devaere *et al.*, 2014). The disarticulated nature of Cambrian skeletal fossils (Small Shelly Fossils or SSFs) generally obscures their placement in the metazoan tree, seemingly awaiting the discovery of exceptionally preserved specimens to unveil their scleritome structure and biological affinity (e.g. Chen *et al.*, 1989; Conway Morris & Peel, 1990; Skovsted *et al.*, 2008, 2009, 2011; Larsson *et al.*, 2014). Such discoveries are however rare and the majority of Cambrian skeletal fossils continue to float in the taxonomic ether, hindering our understanding of the earliest animal ecosystems.

The problems in assessing such skeletal fossils are exemplified by the mobergellans, a group of small, disc-shaped sclerites. Almost flat in lateral profile, the sclerites can be variously convex or concave and exhibit concentric growth lines on the outer surface and are generally considered to be originally phosphatic in composition (Bengtson, 1968; Skovsted, 2003). Historically, this exclusively Cambrian family (consisting of five genera and at least eight species) was one of the first SSF groups documented (Billings, 1871a) and despite attracting considerable interest for over 140 years (Billings, 1871a; Hall, 1872; Moberg, 1892; Hedström, 1923, 1930; Bengtson, 1968; Missarzhevsky, 1989; Rozanov & Zhuravlev, 1992; Conway Morris & Chapman,

1997; Skovsted, 2003; Streng & Skovsted, 2006; Demidenko *et al.*, 2012), our understanding of their functional morphology and biological affinity remains limited.

The most distinctive character of mobergellans is the prominent radiating, roughly bilaterally symmetrical structures on the presumed internal surface (Figs 1A-B, 2A, 4D). These markings, which are the focus of this study, have been interpreted and generally accepted as muscle scars (Moberg, 1892; Bengtson, 1968; Conway Morris & Chapman, 1997; Skovsted, 2003; Streng & Skovsted, 2006) and here we continue to follow this interpretation. The muscle scars in some mobergellans (e.g. *Mobergella holsti* (Moberg, 1892)) are delineated by puncta, visible as fine pores on the inner surface of the sclerite (Bengtson, 1968, fig. 3). This feature however is not ubiquitous across the group (compare *Mobergella holsti* with *Discinella micans* (Billings, 1871a) Fig. 1A, B; see Bengtson, 1968) and appears to be a unique feature without obvious modern analogues. In the absence of key morphological characteristics, the number of muscle scars has been frequently used to decipher the biological function and affinity of mobergellan sclerites (Streng & Skovsted, 2006 and references therein). However, the number of muscle scars displayed by mobergellan taxa varies considerably between genera and even intraspecifically (Bengtson, 1968; Conway Morris & Chapman, 1997; Skovsted, 2003), a feature seldom seen in fossil and extant taxa. For example, *Mobergella holsti* generally bears 13- 14 muscle scars, *Mobergella hexactina* Skovsted, 2003 displays 11-12 scars and *Discinella micans* exhibits 9-10 scars. Given this numerical variation, alternative approaches to studies of mobergellans may be more insightful.

Studies on shell-bearing taxa, such as brachiopods and molluscs, tend to focus predominantly on the variation in shell morphology (e.g. Stanley, 1970; Haney *et al.*, 2001; Gaspar *et al.*, 2002; Inoue *et al.*, 2013) a few studies however, have correlated the

size of muscle attachment sites with life position (e.g. endobyssate verse epibyssate taxa, Stanley 1972), environmental parameters (e.g. high energy verse low energy environments, Colmenar *et al.*, 2014), particular biological functions (e.g. the ability to swim in scallops, Gould, 1971) and behavioural adaptations to specific environments (e.g. burrowing in intertidal molluscs, Ansell & Trevallion, 1969 and in the coral boring species of *Lithophaga*, Morton & Scott, 1980). These studies demonstrate the potential utility of investigating the size of muscle attachment sites in shells, however to help account for intraspecific variation, additional morphological information is regularly used to complement the study (Ansell & Trevallion, 1969; Stanley, 1972; Gould, 1971; Morton & Scott, 1980). Muscle scars are invariably present in mobergellans and represent the only traces of the animal's soft body and complemented with the additional morphological characteristics available (such as size, shape and shell convexity/concavity), we believe they provide our best opportunity to understand their function and affinity.

In the past, comparisons of mobergellans with modern biological groups have relied heavily on the number and distribution of these muscle scars. Mobergellans have been compared to a variety of groups, including brachiopods (Moberg, 1892), monoplacophorans (Poulsen, 1963; Missarzhevsky, 1989), patellacean gastropods (Hedström, 1923; Poulsen, 1932), bivalves (Erwin & Valentine, 2013) and they have also been suggested as potentially forming a dorsal scleritome (Rozanov & Zhuravlev, 1992). Little consensus exists, undoubtedly a consequence of a paucity of comparable morphological characters. An early and lasting functional interpretation is that mobergellan sclerites acted as operculum of some hitherto undiscovered tube-dwelling organism (Billings, 1871a; Åhman & Martinsson, 1965; Bengtson, 1968). The recurrent

nature of this proposal could either partially endorse its legitimacy or merely represents the path of least incongruence.

Documenting biotas from the early Cambrian sheds light on biological diversity, body plan complexity and evolutionary history of many animal groups and is pivotal in understanding the events surrounding one of the greatest biological diversification events in the history of life. It is frustrating that the function of many of the minute skeletal fossils from the early stages of this diversification is unknown and many cannot be assigned with confidence to particular biological groups. Here we investigate the percentage of the sclerite inner surface that is occupied by muscle scars of the two most well known mobergellan taxa, *Mobergella holsti* and *Discinella micans*. The total surface area that the muscle scars constitute, despite their variation in shape and number, is an aspect of the mobergellans that is yet to be investigated. We take the novel approach of comparing muscle scar/inner surface area of the two Cambrian species with the muscle scar/inner surface area ratios of a variety of extant and fossil invertebrate taxa where the functional significance of the shells and scars is known. The aim of our study is to explore whether the total area of the mobergellan muscle scars, complemented with additional morphological information, is consistent with the interpretation that mobergellan sclerites represent opercula.

MATERIAL AND METHODS

Fossil and extant taxa included in this study were specifically chosen as representatives of organisms that mobergellans have been compared to (e.g. two-valved organisms such as bivalves and brachiopods and univalved organisms such as patellacean gastropods and monoplacophorans or suggested as performing a particular function (e.g. dorsal

124 scleritome and operculum). Taxa included exhibit different modes of life and have been
125 investigated in an attempt to better understand the mode of life and function of the
126 mobergellans. Easily distinguishable muscle scars was present on all specimens
127 included in the analysis.

128 Relationships between members of the mobergellid family are unclear and
129 currently unresolved. The group has a complex systematic history and may be in need
130 of thorough revision. However, this would be outside the scope of the present paper and
131 here we follow the interpretations and systematic identifcations of Skovsted (2003) and
132 Streng and Skovsted (2006). The focus of this study are *Mobergella holsti* from the
133 Cambrian of Sweden (Bengtson, 1968) and *Discinella micans* from the Cambrian of
134 Greenland and Labrador, Canada (Skovsted, 2003, 2006). *Mobergella holsti* and *D.*
135 *micans* were chosen for a number of reasons; both taxa are well known in the scientific
136 literature and are undoubtedly considered to be representatives of the Mobergellidae
137 (Skovsted, 2003). Both species also possess distinguishable muscle scars and lastly
138 well-preserved specimens were readily available in the collections of the Swedish
139 Museum of Natural History.

140 We compare the two Cambrian species to a range of fossil and extant species of
141 molluscs, brachiopods and an annelid. Extant species include the elytra of the polynoid
142 annelid *Lepidonotus squamatus* (Linnaeus, 1758), the linguliform brachiopod
143 *Discinisca lamellosa* (Broderip, 1833), the bivalves *Ostrea edulis* Linnaeus, 1758,
144 *Pseudamussium peslutrae* (Linnaeus, 1771) and *Tellina lineata* Turton, 1819, the
145 gastropod limpet *Patella* sp., the operculum of the gastropod genera *Nerita* Linnaeus,
146 1758 and *Natica* Scopoli, 1777 the monoplacophoran *Neopilina galatheae* Lemche,
147 1957 and plates from the polyplacophoran *Chiton tuberculatus* Linnaeus, 1758 (Fig. 1).
148 Analyzed fossils species include four taxa generally considered to be

149 monoplacophorans, the Ordovician species *Pilina cheyennica* Peel, 1977 and *Proplina*
150 *cornutaformis* (Walcott, 1879) and the Silurian species *Tryblidium reticulata*
151 Lindström, 1880 and *Kosovina peeli* Horný, 2004, the operculum of the Ordovician
152 hyolithid *Gompholites striatulus* (Barrande, 1847), plates from the Pliocene
153 polyplacophoran *Callistochiton* spp. (Vendrasco et al., 2012) and the problematic
154 Ordovician two-valved taxon, *Angarella jaworowskii* Asatkin, 1932 (Dzik 2010). For
155 the sake of simplicity all taxa will be referred to by their generic name for the remainder
156 of the paper. All examined specimens, except for *Natica*, *Gompholites*, *Pilina*,
157 *Proplina*, *Kosovina*, *Callistochiton* and *Angarella* (where measurements were obtained
158 from published images) are housed at the Swedish Museum of Natural History, in the
159 Palaeobiology and Zoology Departments (SMNH).
160 The number of each taxon included in the analysis is provided in Figure 3.
161 Rarity and poor preservation resulted in some taxa being represented by few data points
162 (Fig. 3). A single species was chosen for each taxon, with the exception of the opercula
163 of *Nerita* and *Natica* and the chiton *Callistochiton*, where a number of species were
164 utilized to compile a comparable dataset. The genera *Natica* and *Nerita* were chosen as
165 in terms of morphology and ecology, these are well-studied operculum-bearing taxa
166 (Ansell, 1960; Vermeij, 1973, 1976, 1977) and at least for *Nerita* specimens, muscle
167 scars are easily visible and specimens were readily available. For the taxa that possess
168 more than a single valve, for consistency, all measurements were taken from the same
169 valve, for example the right valve in *Ostrea* (see Waller 1981), left valve in
170 *Pseudomussium* (see Hayami & Okamoto, 1986) right valve in *Tellina* (see de Freitas
171 Tallarico *et al.*, 2014), the ventral valve in *Discinisca* (see Williams *et al.*, 2000). For
172 organisms exhibiting an imbricated dorsal sclerite me, only intermediate valves in
173 *Chiton* were examined (see Schwabe 2010), however 4 intermediate valves and 4 tail

174 valves (to test for variability along the dorsal scleritome) were measured from a
175 published report of *Callistochiton* (Vendrasco *et al.*, 2012) and *Lepidonotus* elytra came
176 from a variety of positions along the dorsal trunk of the annelid.
177 The authors recognize that not all muscles possessed by an organism will leave
178 discrete scars, however the general distribution and size of muscle attachment areas, is
179 relatively conservative in related organisms and generally share a comparable functional
180 adaptation (Rudwick, 1970; Stanley, 1977). The authors also acknowledge that the
181 outline of specimens may not capture the exact surface area of the interior.
182 Consequently well-preserved specimens exhibiting a limited topographic profile and
183 without a complex sculpture were utilised to minimalise the error and increase the
184 accuracy of surface area measurements.
185 Specimens were photographed in plan view under normal light using a Canon
186 EOS6D digital SLR camera except for *Mobergella* and *Discinella* that were imaged
187 using SEM facilites at the Swedish Museum of Natural History and at Uppsala
188 University, Sweden. Measurements and calculations were done with ImageJ (1.49v,
189 available online at http://imagej.nih.gov/ij/download.html, National Institutes of Health,
190 USA). The inner surface of each specimen was outlined and the resulting area
191 calculated. Then each muscle scar was outlined and the total resulting area calculated
192 (for an example see *Discinella*, Fig. 2) and the percentage of the total area occupied by
193 the muscle scars was tabulated. Box and beanplots (Table S1) were produced with
194 BoxPlotR (available online at http://boxplot.tylerslab.com/, Spitzer *et al.*, 2014;
195 Krzywinski & Altman, 2014). Subsequent analyses, such as normal probability plots, t-
196 tests, one-way ANOVA and Tukey's Honestly Significant Difference (HSD) test (Table
197 S2) were completed using PAST version 3.1 (Hammer *et al.*, 2001).
198

RESULTS

The percentage of surface area that the muscle scars occupy in relation to the total inner surface area is visually presented as a box (Fig. 3A) and beanplot (Fig. 3B, detailed statistics available in Table S1). The boxplot indicates that *Discinella* and *Mobergella* are very similar in terms of muscle scar percentage with a mean of 19.25 and 18.42 respectively. Normal probability plot correlation coefficients were all above the critical value (e.g. >0.9590 for n=26) indicating the data came from a population with a normal distribution. A t-test also indicates that the measurements obtained from both mobergellan taxa do not significantly differ (*p*-value 0.164).

The boxplot reveals that muscle scar percentage of both mobergellans when compared to the majority of measured taxa is relatively large and Tukey's HSD tests showed significant differences between the mobergellans and nearly all other taxa, with the exception of *Natica* (Table S2). The only overlap of the whiskers of both mobergellan taxa is with the opercula of *Natica* and *Nerita* (Fig. 3A). The area of the attachment scar of *Natica* opercula is very similar to the mobergellans with a mean of 18.9 and the muscle scar percentage of *Nerita* opercula is slightly larger in comparison with a mean of 23.16.

The muscle scar percentage of the remaining taxa, when compared with the mobergellans is considerably lower. The muscle scar area of *Discinisca, Ostrea* and *Pseudomussium* considerably overlap (Fig. 3A) and there is also some degree of overlap in whisker length between the bivalve *Tellina* and the limpet *Patella*. There is little difference between the two polyplacophorans, *Chiton* and *Callistochiton* and of particular note are the similarities in measurements from the intermediate valves of *Callistochiton* which are basically identical to the tail valves (Fig 3A). The extant

monoplacophoran taxa, *Neopilina* exhibits a low muscle scar percentage of 5.18, significantly lower than the four fossil monoplacophorans.

In a general trend, the three taxa possessing an imbricating dorsal scleritome (*Lepidonotus*, *Chiton* and *Callistochiton*) exhibited the lowest muscle area to sclerite area percentage, followed by the taxa that possess two shells (*Ostrea*, *Pseudomussium*, *Discinisca* and *Tellina*) and the largest muscle area percentage is displayed by the mobergellans and the opercula of *Nerita* and *Natica*. This pattern is punctuated by the opercula of the Ordovician hyolithid *Gompholites* that possesses a series of small muscle scars that constitute a mean of 4.14 and the limpet *Patella* that possesses a single horseshoe-shaped scar with a mean of 9.37.

For a visual comparison of the individual observations and the density of the distributions a beanplot (Kampstra, 2008) has been provided (Fig. 3B). Beanplots display all individual observations (unlike Boxplots) in a one-dimensional plot, but also show the estimated density of distributions and the average (Kampstra, 2008). The variation of the mobergellan muscle area percentage is apparent and both taxa display a similar distribution of individual measurements. The mobergellans also have the highest standard deviation (s.d.) of 2.1 and 2.0 respectively, followed by *Patella* (1.66) and the opercula of *Nerita* (1.6) compared with *Lepidonotus* that recorded the lowest s.d. of 0.44 (Table S1). In terms of individual observations, the only taxa that exhibits measurements that overlap with *Discinella* and *Mobergella* is the opercula of *Nerita* and *Natica*.

DISCUSSION

The study presented here represents the first investigation into the total area occupied by the muscle scars relative to the inner surface area of mobergellan sclerites, comparing directly the muscle scar area of other fossil and extant taxa. Our results show clearly that compared to the majority of taxa analyzed, the percentage of internal surface area that the muscle scars occupy in mobergellan sclerites is larger. In relative size it is only comparable to the muscle scar area observed on the opercula of the gastropod genera *Natica* and *Nerita*. The size of the attachment sites indicates that the construction of the muscles would represent a significant investment to the organism and certainly had important functional significance. Based on our data and a review of similar structures in fossil and extant organisms we herein discuss evidence for and against a number of potential functional hypotheses for mobergellan sclerites.

MOBERGELLANS AS TWO-VALVED ORGANISMS

Mobergellans have been suggested as representing valves from a variety of two-valved organisms. Early comparisons of mobergellans to the crown-group brachiopods were based on the similarities in shell composition to Cambrian linguliform brachiopods (Hall, 1872). The similarity in musculature arrangement prompted Dzik (2010) to make comparisons with the two-valved *Angarella*, a possible ancestor to the cephalopods and Erwin & Valentine (2013) recently claimed, without explanation, that *Mobergella* is a stem bivalve. From our results, what is immediately apparent is that the mean of the muscle scar area for all four two-valved taxa represent approximately one half to a third of the mean of the muscle scar measurements of the mobergellans.

The unique distribution of muscle scars in mobergellans does bear a resemblance to the problematic two-valved taxon *Angarella*, described from the Ordovician of Siberia (Dzik, 2010). The dorsal valves of *Angarella* are conical and

display 5 paired scars and a narrow posterior scar (Dzik, 2010, fig. 4). The ventral valve is flat, bearing a pair of elongate muscle scars and has been interpreted has having been cemented to hard substrates (Dzik, 2010). Despite differences in shell composition (phosphatic verse calcitic), Dzik (2010) noted similarities in the musculature and hypothesized that mobergellans may have also been a two-valved organism, cementing their 'ventral' valve to hard substrates in a manner akin to *Angarella*. The percentages of the inner surface shell area that the scars constitute are markedly different though; *Angarella* with a much lower mean of 11.09 compared to the mobergellans 19.25 and 18.42 respectively and there is no additional evidence to support a cemented lifestyle for mobergellans.

Two-valved taxa are morphologically diverse, with a vast array of body plans and life habits. Despite the wide range of life habits and variation in musculature arrangement exhibited by the two-valved taxa investigated herein, all display similar muscle scar measurements and individual observations largely overlap (Fig. 3B). The four genera however contrast markedly in valve morphology and musculature distribution (Fig. 1D-F, I) and represent a scenario where the subtle differences in the muscle scar area cannot alone resolve the function and affinity of the skeletal element and any interpretation would benefit from additional morphological information. A smaller area occupied by musculature would provide more space for the remaining soft parts and increase the probability that the organism could enclose its entire body within the shell. The ability to close the shell and isolate the internal body of the organism from outside stresses would be pivotal for the survival of the individual.

Due to the lack of correlation in muscle size we consider it unlikely, based on existing morphological evidence, that mobergellans constitute part of a two-valved organism This is of course assuming, in a two-valved scenario that both valves are

morphologically recognizable as mobergellan sclerites. The number and distribution of muscle scars of mobergellans is not known from extant two-valved taxa and the large area occupied by muscle scars and the almost flat (or sometimes concave) lateral profile of the mobergellan discs (Fig. 4E-G), is not consistent with possessing the capability of sheltering the entire soft body within a two-valved organism.

MOBERGELLANS AS UNIVALVED ORGANISMS

Hedström (1923, 1930) suggested that mobergellans represent molluscan shells and more recently, Conway Morris & Chapman (1997, p. 977) advocated that of 'all the metazoan groups, comparisons with the molluscs could be the most fruitful line of further investigation'. The principal reasoning behind this championing of a molluscan affinity is the striking similarities in the pattern of muscle scars of some mobergellans and the single shelled monoplacophorans (Hedström, 1923, 1930). Both groups display a circumferential distribution of muscle scars and at first glance they do bear a putative similarity. However the similarities are rather superficial. Muscle attachment sites in the two groups differ not only in number (Yochelson, 1958; Peel, 1977; Conway Morris & Chapman, 1997; Horný, 2004; Lindberg, 2009; Ruthensteiner *et al.*, 2010), but also significantly in the area that the attachment sites occupy (Fig. 3). The Palaeozoic monoplacophorans, including *Tryblidium* (holotype of the type species reproduced here Fig. 1k with six pairs of muscle scars) all have muscle scars occupying much of the same proportion (11.3% - 12.5%) of the inner surface of the shell. The sites of muscle attachment in the single analyzed extant species, *Neopilina* is considerably smaller in terms of area, only occupying 5.1% (Fig. 3A) of the inner surface area, despite the possession of eight pairs of muscle scars (Lemche & Wingstand, 1959). The reason for this difference in muscle attachment area in the extant monoplacophorans compared

323 with their fossil equivalents is unclear. As a result of possessing thin shells, muscle
324 scars are rarely observed on extant forms and Lemche & Wingstand (1959) based their
325 schematic illustration of *Neopilina* on the muscle scar arrangement of fossil
326 monoplacophorans. Shells of *Neopilina* were investigated during this study, but no scars
327 were observed and measurements taken for this analysis were done from the schematic
328 illustration of Lemche & Wingstand (1959). This may to some degree explain the
329 discrepancies in muscle attachment size between extant and fossil monoplacophorans.
330 With each fossil and extant monoplacophoran represented by a single data point, a
331 larger data set would be necessary to solve this problem. However, it is also possible
332 that muscle scar area is related to changes in habitat, as extant monoplacophora
333 predominantly live at abyssal depths (Lemche & Wingstrand, 1959; Lindberg, 2009)
334 contrasting with Palaeozoic taxa that are typically recovered from much shallower,
335 limestone settings (e.g. Peel, 1977; Horný, 2004).
336 Compared to the mobergellans (mean percentage of 19.25 and 18.46
337 respectively) the results from the single shelled monoplacophorans are considerably
338 lower. Furthermore, the shells of mobergellans and monoplacophorans contrast notably
339 in shape and the position of the apex (overhanging the anterior margin in
340 monoplacophorans compared to sub-central in mobergellans). With the exception of
341 possessing a set of radiating muscle scars, similarities between the groups are few. The
342 other single shelled organism included in the analysis, the gastropod limpet *Patella*
343 exhibits a single, horseshoe-shaped muscle scar (Fig. 1J). With a mean of 9.37%, the
344 muscle attachment area of *Patella* is approximately half of the mean of *Mobergella* and
345 *Discinella* (Fig. 3). Furthermore, the flattened mobergellan shells do not support a
346 limpet-like reconstruction, as previously noted by Åhman & Martinsson (1965) and
347 Bengtson (1968). Lacking a second shell to sufficiently enclose their soft parts, taxa that

possess only a single shell (e.g. limpet gastropods and monoplacophorans) alternatively utilize the substrata (e.g. rock surfaces) to protectively seal their soft parts within their shell (Vermeij, 1973, 1976, 1977). A similar explanation for the relatively small area of the inner shell occupied by muscle scars can be given for univalved taxa as for two-valved taxa. Except for the muscle scars, nothing is known about the soft parts of mobergellans and an immediate dismissal of monoplacophoran similarities may be unwarranted. However, the large area occupied by the muscle scars and the flat to sometimes concave profile of mobergellan sclerites is not consistent with mobergellans representing univalved organisms.

THE FORMATION OF A DORSAL SCLERITOME

The discovery of *Microdictyon sinicum* Chen, Hou & Lu, 1989 and *Halkiera evangelista* Conway Morris & Peel, 1995 revolutionized the interpretation of Cambrian skeletal assemblages. Both discoveries providing a model for disarticulated sclerites, resulting in a host of skeletal fossils interpreted as constituting cataphract dorsal shields of vermiform bilaterians (Evans & Rowell, 1990; Williams & Holmer, 2002; Li & Xiao, 2004). Even, mobergellans have been suggested to represent disarticulated sclerites from a larger dorsal scleritome (Rozanov & Zhuravlev, 1992) but evidence to support this hypothesis is particularly tenuous. Three taxa were investigated in this study that possess a dorsal scleritome, the polyplacophorans *Chiton* and *Callistochiton* and the polynoid annelid *Lepidonotus*. Curiously all investigated dorsal scleritome bearing taxa exhibit near identical and very low results (3.7% - 5.4%), show a very low standard deviation (Table S1) and minimal variation in muscle attachment area along the dorsal scleritome (Fig. 3).

372 Elytra vary noticeably in shape and size, depending on their location on the
373 trunk and elytra representing a variety of positions along the dorsal trunk of
374 *Lepidonotus* has been included in the analysis. *Lepidonotus* scars displayed a low
375 degree of variation (s.d. 0.44) indicating the area that the attachment site is proportional
376 to the size of the sclerite along the length of the dorsal scleritome. Curiously the other
377 investigated dorsal scleritome bearing taxa, *Chiton* and *Callistochiton* also exhibits a
378 relatively small muscle attachment area (a mean of 5.4% and 4.6% respectively).
379 Despite the intermediate and tail valves of *Callistochiton* exhibiting a different number
380 of muscle attachment areas (Vendrasco *et al.* 2012) the measurements were nearly
381 identical (intermediate mean 4.6% and tail mean 4.7%) also indicating minimal
382 variation in muscle attachment area along the dorsal scleritome.
383 The principal difficulty with the proposal that mobergellan sclerites formed part
384 of a larger scleritome is the number of muscle scars and the large area on the inner
385 surface of the shell that the musculature occupies. Sites of muscle attachment have not
386 been documented on the internal surface of most sclerites that are definitely known to
387 have formed part of the dorsal scleritome in Cambrian taxa (e.g. Wrona, 1987;
388 Bengtson *et al.*, 1990; Müller & Hinz-Schallreuter, 1993; Zhang & Aldridge, 2007;
389 Topper *et al.*, 2011, 2013; Caron *et al.*, 2013; Barragán *et al.*, 2014), despite
390 *Microdictyon* sclerites having been suggested as reinforced areas of muscle attachment
391 (Budd, 2001). Given their size and prominence, the energy invested by the mobergellan
392 organism to construct and maintain such musculature attachments seems excessive for
393 the formation of a multi-element scleritome. Furthermore there is no morphological
394 evidence that indicates that mobergellans shells were juxtaposed to other sclerites or
395 overlapping in an imbricating dorsal scleritome. Mobergellan sclerites are usually
396 almost perfectly circular (Figs 1A-B, 4D) and show no consistent signs of smoothing or

grinding on the exterior of the shell that could imply that the shells were in contact during life. Conjoined specimens have also never been found (unlike among other Cambrian sclerites, e.g. Demidenko, 2004; Skovsted *et al.*, 2015) and mobergellans do not possess any shell extensions that would enhance the suturing of the valves, as seen in extant chitons (Todt *et al.*, 2008; Schwabe, 2010).

THE OPERCULUM HYPOTHESIS

The interpretation that mobergellans represent the operculum of a tube dwelling organism has been the ominous cloud lingering over the enigmatic sclerites since the 1870s (Billings, 1871a). Only limited evidence has been presented to support this hypothesis (Bengtson, 1968) and the enduring nature of the proposal is seemingly one of least discordance. There are however many lines of evidence to support the claim. Tubular fossils of similar phosphatic composition are frequent constituents of Cambrian assemblages (Bengtson *et al.*, 1990; Wrona, 2004; Skovsted, 2006; Topper *et al.*, 2009; Skovsted & Peel, 2011) and the circular shape of mobergellan sclerites and their tendency to display flared margins and sometimes concave shapes would also appear consistent with life within a tube. Our analysis also supports this hypothesis, with the muscle scars of gastropod opercula being the only taxa analyzed with a somewhat comparable area of the inner shell occupied by muscle scars (Fig 3).

However, in our analysis, not all opercula exhibit large muscle scars on their internal surface, as shown by the operculum of the Ordovician hyolithid *Gompholites* (Martí Mus & Bergström, 2005). This disparity can be explained by the contrasting functions that hyolithid opercula and gastropod opercula perform. Hyolithids possessed a complex musculature system that was used to open and close their opercula but also likely to provide a wide range of movement to other skeletal elements, the helens,

422 primarily for orientation and stabilization (Martí Mus & Bergström, 2005, 2007; Martí
423 Mus *et al.*, 2014). Further, hyolithid opercula exhibit prominent internal projections,
424 clavicles and cardinal processes (Marti Mus & Bergström, 2005) that presumably
425 functioned as levers for muscular action, effectively reducing the force (and hence
426 muscular size) needed to perform functions such as closing the aperture of the conch.
427 Based on musculature comparisons, there is no evidence to suggest that the mobergellan
428 shells functioned in a similar manner to hyolithid opercula, providing leverage and
429 articulating other skeletal elements for movement.
430 Gastropod opercula on the other hand are primarily used to close the aperture of
431 the shell when the organism has withdrawn (Vermeij, 1971; Hunt, 1976; Checa &
432 Jiménez-Jiménez, 1998; Vermeij & Williams, 2007). The tight closure of the shell in
433 *Nerita* for example, offers protection and assists in the avoidance of water loss and
434 subsequent desiccation during periods of exposure (Vermeij, 1971, 1973). Naticids as
435 predatory gastropods, display a very different lifestyle to the grazing neritids (Ansell,
436 1960; Berry, 1982; Hughes, 1985), yet they employ their opercula in a similar manner,
437 sealing their aperture in times of environmental or predatory stress. The overlap of
438 individual observations (Fig. 3) suggests that mobergellan sclerites may have
439 functioned as an operculum of an organism, closing the aperture during times of
440 predatory or desiccation stress. There is presently no evidence, to suggest that
441 mobergellan sclerites are opercula of a gastropod. However, representing attachment to
442 a portion of the organism rather than housing the entire body of the animal, would
443 resolve the mobergellan conundrum of concave shells and would also explain the
444 relative high percentage of the internal surface area that is utilized by musculature. The
445 large area of the opercula inner surface occupied by muscle scars (Figs 1H, 3) is a
446 reflection of the strength in which the individual seals the aperture in times of stress

447 (Vermeij 1973; Kaim and Sztajner 2005) and the attachment area of some gastropod
448 species can constitute nearly 50% of the total area (Pimenta *et al*., 2008). Therefore we
449 suggest that mobergellans were opercula employed to firmly seal the aperture and
450 protect the presumably tube-dwelling animal.

451 The major stumbling block of the operculum hypothesis has been the apparent
452 lack of a corresponding co-occurring tube. Why would an organism housed in a tube of
453 negligible preservation potential possess a relatively thick, densely laminated
454 phosphatic operculum? While not fatal to the hypothesis, the absentee tube has
455 presented a hurdle that is challenging to negotiate. Phosphatic tubes, such as
456 hyolithellids are extremely common constituents in Cambrian faunal assemblages,
457 (Billings, 1871b; Bengtson *et al*., 1990; Skovsted, 2006: Topper *et al*., 2009; Skovsted
458 & Peel, 2011; Devaere *et al*., 2014) yet are rarely associated with mobergellans. There
459 have been a few occurrences where phosphatic tubes and mobergellan sclerites co-
460 occur, such as New York (Lochman, 1956; Landing & Bartowski, 1996), Siberia
461 (Rozanov & Zhuravlev, 1992) and Greenland (Skovsted, 2006). Re-examination of
462 material from Venenäs, Sweden (Åhman & Martinsson, 1965; Bengtson, 1968, Fig. 4A-
463 D) has also revealed a few phosphatic tubes that are comparable in size to mobergellan
464 sclerites (Fig. 4A-C). Despite these glimpses of association between tube and possible
465 operculum, it is not a persistent occurrence.

466 The dearth of tubes co-occurring with mobergellan sclerites could be explained
467 by speculating that the organism lived attached to the substrate and that after death and
468 soft part decomposition, the opercula were whisked away by currents and transported to
469 their place of deposition. Here we suggest that the tube may have been cemented or at
470 least firmly attached to the substrate and remaining attached after the death and decay of
471 the animal. The opercula would eventually dissociate from the decaying organism and

472 be transported away, leaving the tube behind. Significantly, mobergellan sclerites have
473 a tendency to be recovered from transported sediments, such as turbidite deposits,
474 debris surrounding archaeocyathan bioherms or in relatively coarse reworked
475 siliciclastic settings (see Table 1). Retrieval from transported and reworked sediments
476 could explain the dissociation between tube and sclerite, if the tube remained firmly
477 attached to the substrate in its original environment. In many faunal assemblages where
478 mobergellan sclerites are present, they are present in an extreme abundance (Table 1). It
479 is worth considering that the high accumulation of mobergellan specimens in many
480 samples (Table 1) could be a result of the transportation and sorting of detached
481 opercula from a gregarious shallow-water tube-dwelling animal. A similar case of
482 dissociation is recognized in fossil assemblages of serpulid opercula and tubes that are
483 seldom found in association (Ippolitov *et al.*, 2014).
484 A wide variety of phopshatic tubes frequently occur in Cambrian
485 deposits, the large majority of which have an unknown biological affinity. The
486 phosphatic tubes from Venenäs exhibit diameters that range from 1.2 mm to 2.5 mm
487 (Fig. 4A-C) and although this size range is comparable to the width of individual
488 sclerites, larger mobergellan specimens have been documented (Bengtson, 1968),
489 including a specimen with a diameter of 6.4-6.5 mm (Åhman & Martinsson, 1965, p.
490 147). Larger phosphatic tubes are known from Greenland (diameter: 4.2 mm; Skovsted
491 & Peel 2011) and even larger but flattened tubes are known from for example the
492 Burgess Shale of British Columbia, Canada (Skovsted & Peel 2011). The taxonomy of
493 phosphatic tubes is problematic (see Skovsted, 2003; Topper et al. 2009; Skovsted &
494 Peel 2011) and the fragmentary nature of the Venenäs tubes precludes a precise
495 taxonomic assignment. Phosphatic tubes are one of the most abundant and widely
496 dispersed forms in the Cambrian and may include a range of quite distantly related

497 forms (see discussion in Skovsted & Peel 2011) and assigning mobergellans to a
498 particular taxonomic group of phosphatic tubes would be somewhat ambitious. A
499 definitive relationship between mobergellans and phosphatic tubes would be difficult to
500 establish without finding an articulated specimen, but the co-occurrence of tubes and
501 sclerites does provide some optimism for future studies. Despite this, a major limitation
502 lingers and that is that the biological affinity of the mobergellans remains unanswered.
503 Whilst there is convincing evidence to support the mobergellan shell having functioned
504 as an operculum there is currently insufficient evidence to place the Cambrian fossil
505 into any known biological group.
506
507 CONCLUSIONS
508
509 Mobergellans lack a broad suite of distinguishing morphological characters, however
510 the sheer size of the muscle scars expressed on the internal surface of the shell stresses
511 that the muscle system must have held an important functional significance. The muscle
512 scars of the mobergellans *Mobergella holsti* and *Discinella micans* are very similar
513 occupying nearly 20% of the total inner surface of the sclerite. The large area occupied
514 by muscle scars, the distribution of the muscle scars, the lateral profile and the
515 composition of mobergellan sclerites is not compatible with representing a univalved
516 mollusc or a single shell of a brachiopod or another two-valved organism. The large
517 muscle scar area and the lack of comparable structures in Cambrian taxa also do not
518 provide any evidence to suggest that the sclerites formed part of a dorsal scleritome.
519 The area that the muscle scars constitute in mobergellen sclerites however, is
520 comparable to the muscle scars on the opercula of gastropods. Combined with their
521 circular shape and the tendency of valves to be variously convex, flat or concave with

522 flared margins, the sclerite morphology appears consistent with life in a tube. Gastropod
523 opercula are utilized to seal the aperture and enclose the entire soft body of the
524 organism inside the shell in times of predatory or desiccation stress. The similarities in
525 muscle scar area suggest that mobergellans could have performed a similar function.
526 The dissociation of the tube and mobergellan sclerties in fossil assemblages is likely a
527 result of transportation, as mobergellan shells are invariably documented from reworked
528 and transported sediments. The organism would have lived in a tube firmly attached to
529 the substrate in shallow water environments. The opercula becoming detached after
530 death and carried away in the currents, leaving the tube still firmly attached to substrate.
531 Despite these advances in regards to the function of the sclerites, there still remains
532 insufficient evidence to place the mobergellans in the metazoan tree and their biological
533 affinities continue to be shrouded in mystery.
534

535 ## ACKNOWLEDGEMENTS

536

537 We are grateful to Stefan Bengtson (Swedish Museum of Natural History, SMNH) for
538 access to mobergellan specimens that were collected from the Cambrian of Sweden
539 over 50 years ago. We also must thank Lena Gustavsson and Anna Persson for
540 permission to wander through the annelid and mollusc collections at the Department of
541 Zoological, SMNH. We also thank Luke Strotz (Yale University) for statistical
542 assistance and Harry Mutvei (SMNH) and Steffen Kiel (SMNH) for insightful
543 discussion. The SMNH and COFUND fellowship (Durham University) is thanked for
544 funding and the manuscript benefited from constructive reviews by five anonymous
545 reviewers.
546

REFERENCES

Åhman E, Martinsson A. 1965. Fossiliferous Lower Cambrian at Äspelund on the Skäggenäs Peninsula. *Geologiska Föreningens I Stockholm Förhandlingar* **87:**139-151

Ansell, A.D. 1960. Observations on predation of *Venus striatula* (Da Costa) by *Natica alderi* (Forbes). *Journal of Molluscan Studies* **34:** 157-164.

Ansell AD, Trevallion A. 1969. Behavioural adaptations of intertidal molluscs from a tropical sandy beach. *Journal of Experimental Marine Biology and Ecology* **4:** 9-35.

Asatkin BP. 1932. Ecardines from the Lower Silurian of the Siberian Platform. *Izvestiia V Sesoiuznogo Geol Razv Obedinenia* **5**: 483-495.

Barragán T, Esteve J, García-Bellido DC, Zamora S, Álvaro JJ. 2014. New Middle Cambrian palaeoscolecid sclerites of *Hadimopanella oezgueli* from the Cantabrian Mountains, northern Spain. *GFF* **136:** 22-25.

Barrande J. 1847. Pugiunculus, ein fossils Pteropoden Geschlecht. *Neues Jahrbuch für Min Geognoise Geol und Petref* **1847:** 554-558.

Bengtson S. 1968. The problematic genus *Mobergella* from the Lower Cambrian of the Baltic area. *Lethaia* **1:** 325-351.

Bengtson S, Conway Morris S, Cooper BJ, Jell PA, Runnegar BN. 1990. Early Cambrian fossils from South Australia. *Memoirs of the Association of Australasian Palaeontologists* **9**, pp. 364.

Berry AJ. 1982. Predation by *Natica maculosa* Lamarck (Naticidae: Gastropoda) upon the trochacean gastropod *Umbonium vestiarium* (L.) on a Malaysian shore. *Journal of Experimental Marine Biology and Ecology* **64:** 71-89.

Billings E. 1871a. On some new species of Palaeozoic fossils. *The Canadian Naturalist (New Series*) **6**: 213-222, 240.

Billings E. 1871b. Proposed new genus of Pteropoda [*Hyolithellus*]. The *Canadian Naturalist* **6**, pp. 240.

Broderip WJ. 1833. New species accompanied by characters. *Proceedings of the Zoological Society of London* **1:** 4-8.

Budd GE. 2001. Why are arthropods segmented? *Evolution and development* **3**, 332-342.

Caron JB, Smith MR, Harvey TH. 2013. Beyond the Burgess Shale: Cambrian microfossils track the rise and fall of hallucigeniid lobopodians. *Proceedings of the Royal Society B: Biological Sciences* **280:** 20131613.

595 **Checa, AG, Jiménez-Jiménez, AP. 1998.** Constructional morphology, origin, and
596 evolution of the gastropod operculum. *Paleobiology* **24:** 109-132.
597
598 **Chen J-Y, Hou X-G, Lu H-Z. 1989.** Early Cambrian netted scale-bearing wormlike
599 sea animal. *Acta Paleontologica Sinica* **28:** 1-16.
600
601 **Colmenar J, Harper DA, Villas E. 2014.** Morphofunctional analysis of *Svobodaina*
602 species (Brachiopoda, Heterorthidae) from south- western Europe. *Palaeontology* **57:**
603 193-214.
604
605 **Conway Morris S, Peel JS. 1995.** Articulated halkieriids from the Lower Cambrian of
606 north Greenland and their role in early protostome evolution. *Phil. Trans: Biol. Sciences*
607 **347:** 305-358.
608
609 **Conway Morris S, Chapman AJ. 1997.** Mobergellans from the Lower Cambrian of
610 Mongolia, Sweden, and the United States: molluscs or opercula of *incertae sedis*?
611 *Journal of Paleontology* **71:** 968-984.
612
613 **de Freitas Tallarico L, Passos FD, Machado FM, Campos A, Recco-Pimentel SM,**
614 **Introíni GO. 2014.** Bivalves of the São Sebastião Channel, north coast of the São Paulo
615 State, Brazil. *Check List* **10:** 97-105.
616
617 **Demidenko YE. 2004.** New data on the sclerite morphology of the tommotiid species
618 *Lapworthella fasciculata*. *Palontological Zhurnal* **38:** 134-140
619

Demidenko YE, Parkhaev PY, Rozanov AY. 2012. Morphological variability and types of preservation of *Mobergella radiolata* – a potential index species for the GSSP of Cambrian Stage 3. In: Zhao YL, Zhu MY, Peng J, Gaines RR, Parsley RL eds. *Cryogenian-Ediacaran to Cambrian Stratigraphy and Paleontology of Guizhou, China*. Journal of Guizhou University, Natural Science 29, pp. 157-158.

Devaere L, Clausen S, Monceret E, Tormo N, Cohen H, Vachard D. 2014. Lapworthellids and other skeletonised microfossils from the Cambrian Stage 3 of the northern Montagne Noire, southern France. *Annales de Paléontologie* **100:** 175-191.

Dzik J. 2010. Brachiopod identity of the alleged monoplacophoran ancestors of cephalopods. *Malacologia* **52:** 97-113.

Erwin DH, Valentine JW. 2013. The Cambrian Explosion. Roberts and Company Publishers, Colorado.

Evans KR, Rowell AJ. 1990. Small shelly fossils from Antarctica: an Early Cambrian faunal connection with Australia. *Journal of Paleontology* **64:** 692-700.

Gaspar MB, Santos MN, Vasconcelos P, Monteiro CC. 2002. Shell morphometric relationships of the most common bivalve species (Mollusca: Bivalvia) of the Algarve coast (southern Portugal). *Hydrobiologia* **477:** 73-80

Gould SJ. 1971. Muscular mechanics and the ontogeny of swimming in scallops. *Palaeontology* **14:** 61-94.

Hall J. 1872. Notes on some new or imperfectly known forms among the Brachiopoda. etc. - *Annual Report to the Regents of the University of the State of New York, Report 23, Appendix G*: 244-247.

Haney RA, Mitchell CE, Kim K. 2001. Geometric morphometric analysis of patterns of shape change in the Ordovician brachiopod *Sowerbyella*. *Palaios* **16:** 115-125.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST-Palaeontological statistics. www. uv. es/~ pardomv/pe/2001_1/past/pastprog/past. pdf, acessado em, 25(07), 2009.

Hayami I, Okamoto T. 1986. Geometric regularity of some oblique sculptures in pectinid and other bivalves: recognition by computer simulations. *Paleobiology* 433-449.

Hedström H. 1923. On "*Discinella holsti* Mbg." and *Scapha antiquissima* (Markl.) of the division Patellacea. *Sveriges Geological Underskrift (C)* **313:** 1-13

Hedström H. 1930. *Mobergella* versus *Discinella*; *Paterella* versus *Scapha* & Archaeophiala (some questions on nomenclature). *Sveriges Geological Undersökning (C* **362:** 1-8.

Horný RJ. 2004. *Kosovina*, a new Silurian tryblidiid genus (Mollusca, Tergomya) from Bohemia (Czech Republic). *Acta Musei Nationalis Pragae, Series B, Natural History* **60:** 143-148.

670

671 **Hughes RN. 1985**. Predatory behaviour of *Natica unifasciata* feeding intertidally on
672 gastropods. *Journal of Molluscan Studies* **51:** 331-335.
673
674 **Hunt S. 1976.** The gastropod operculum: a comparative study of the composition of
675 gastropod opercular proteins. *Journal of Mollusca Studies* **42:** 251-260.
676
677 **Inoue K, Hayes DM, Harris JL, Christian AD. 2013.** Phylogenetic and morphometric
678 analyses reveal ecophenotypic plasticity in freshwater mussels *Obovaria jacksoniana*
679 and *Villosa arkansasensis* (Bivalvia: Unionidae). *Ecology and Evolution* **3:** 2670-2683
680
681 **Ippolitov AP, Vinn O, Kupriyanova EK, Jäger M. 2014.** Written in stone: history of
682 serpulid polychaetes through time. *Memoirs of the Museum of Victoria* **71:** 123-159.
683
684 **Kaim A, Sztajner P. 2005**. The opercula of neritopsid gastropods and their
685 phylogenetic importance. *Journal of Molluscan Studies* **71:** 211-219.
686
687 **Kampstra P. 2008**. Beanplot: A boxplot alternative for visual comparison of
688 distributions. *Journal of statistical software* **28:**.1-9.
689
690 **Koneva, SP. 1983.** Mobergella iz nizhnego kembriya seletinskogo sinklinoriya.
691 *Stratigrafiya i paleontologiya niznego paleozoya Kazakhstana,* 110-112.
692
693 **Krzywinski M, Altman N. 2014.** Points of significance: Visualizing samples with box
694 plots. *Nature methods* **11:** 119-120.

695

696 **Landing E, Bartowski KE. 1996.** Oldest shelly fossils from the Taconic allochthon
697 and late Early Cambrian sea-levels in eastern Laurentia. *Journal of Paleontology* **70:**
698 741-761.

699

700 **Larsson CM, Skovsted CB, Brock GA, Balthasar U, Topper TP, Holmer LE. 2014.**
701 *Paterimitra pyramidalis* from South Australia: scleritome, shell structure and evolution
702 of a lower Cambrian stem group brachiopod. *Palaeontology* **57:** 417-446.

703

704 **Lemche H. 1957.** A new living deep-sea mollusc of the Cambro-Devonian class
705 Monoplacophora. *Nature* **179:** 413-416.

706

707 **Lemche H, Wingstand KG. 1959.** The anatomy of *Neopilina galatheae* Lemche, 1957
708 (*Mollusca, Tryblidiacea*). *Galathea Report, Copenhagen* **3:** 9-71.

709

710 **Li G, Xiao S. 2004.** *Tannuolina* and *Micrina* (Tannuolinidae) from the Lower
711 Cambrian of eastern Yunnan, South China, and their scleritome reconstruction. *Journal*
712 *of Paleontology* **78:** 900-913

713

714 **Lindberg DR. 2009.** Monoplacophorans and the origin and relationships of mollusks.
715 *Evolution: Education and Outreach* **2:** 191-203.

716

717 **Lindström G. 1880.** Fragmenta silurica. Samson & Wallin, Stockholm.

718

719 **Linnaeus CV. 1758**. Systema naturae per regna tria naturae, secundum classes, ordines,

720 genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 10, Tomus 1. L.
721 Salvii, Stockholm, Sweden, pp. 823.
722
723 **Linnaeus CV. 1771.** Regni animalis, Appendix. *Insecta*, pp. 529-543.
724
725 **Lochman, C.** 1956. Stratigraphy, paleontology and paleogeography of the
726 *Elliptocephala asaphoides* strata in Cambridge and Hoosick Quadrangles, New York.
727 *Bulletin of the Geol Soc of America* **67**: 1331-1396.
728
729 **Martí Mus M, Bergström J. 2005**. The morphology of hyolithids and its functional
730 implications. *Palaeontology* 48:1139-1167
731
732 **Martí Mus M, Bergström J. 2007.** Skeletal microstructure of helens, lateral spines of
733 hyolithids. *Palaeontology* **50:** 1231-1243.
734
735 **Martí Mus M, Jeppsson L, Malinky JM. 2014.** A complete reconstruction of the
736 hyolithid skeleton. *Journal of Paleontology* **88:** 160-170.
737
738 **Missarzhevsky, VV** 1976. Novye dannye o rannekembriyskikhmonoplakoforakh.
739 *Paleontologischeskij Zhurnal* **1976**: 129-131.
740
741 **Missarzhevsky VV 1989**. Drevnejshie skeletnye okamenelosti i stratigrafiya
742 pogranichnykh tolshch dokembriya i kembriya. *Trudy Geolog Inst AN SSSR* **443:** 1-237.
743
744 **Moberg JC. 1892**. Omen nyupptickt fauna i block af kambrisk sandsten, insamlade av

745 Dr. N.O. Holst. *Geologiska Föreningens I Stockholm Förhandlingar* **14:** 103-120.
746
747 **Morton B, Scott PJB. 1980.** Morphological and functional specializations of the shell,
748 musculature and pallial glands in the Lithophaginae (Mollusca: Bivalvia). *Journal of*
749 *Zoology* **192:** 179-203.
750
751 **Müller K, Hinz-Schallreuter I. 1993**. Palaeoscolecid worms from the Middle
752 Cambrian of Australia. *Palaeontology* **36:** 549-591.
753
754 **Palmer, AR. 1971**. The Cambrian of the Appalachian and eastern New York regions,
755 eastern United States. In: CH. Holand ed., *Cambrian of the New World*. Wiley-
756 Interscience, New York, 169-217.
757
758 **Peel JS. 1977.** Relationship and internal structure of a new *Pilina* (Monoplacophora)
759 from the late Ordovician of Oklahoma. *Journal of Paleontology* **51:** 116-122.
760
761 **Pimenta AD, do Couto DR, Santos Costa PM. 2008.** A new species and a new record
762 of Muricidae (Gastropoda) from Brazil: genera *Pterynotus* and
763 *Leptotrophon*. *Nautilus* **122:** 244-251.
764
765 **Poulsen C. 1932.** The Lower Cambrian faunas of East Greenland. *Meddelelser om*
766 *Grønland* **87**, no. 6.
767

Poulsen V. 1963. Notes on Hyolithellus Billings, 1871, Class Pogonophora Johannson, 1937. i kommission hos Ejnar Munksgaard. Biologiske Meddelelser udgivet af Det Kongelige Danske Videnskabernes **Selskab 23:** 1-15.

Rozanov AY, Zhuravlev AY. 1992. The Lower Cambrian fossil record of the Soviet Union. In: Lipps JH, Signor PW eds. *Origin and early evolution of the Metazoa*, New York (Plenum Press), pp. 205-282.

Rudwick MJS. 1970. Living and Fossil Brachiopods. London: Hutchinson and Co.

Ruthensteiner B, Schröpel V, Haszprunar G. 2010. Anatomy and affinities of *Micropilina minuta* Warén, 1989 (Monoplacophora: Micropilinidae). *Journal of Molluscan Studies* **76:** 323-332.

Schwabe E. 2010. Illustrated summary of chiton terminology. *Spixiana* **33:** 171-194.

Scopoli, JA. 1777. Introductio ad Historiam Naturalem Sistentes Genera Lapidium, *Plantarum et Animum*. *Vol. 6*. Prague, p. 506.

Skovsted CB. 2003. Mobergellans (problematica) from the Cambrian of Greenland, Siberia and Kazakhstan. *Paläontogische Zeitschrift* **77:** 429-443.

Skovsted CB. 2006. Small Shelly fauna from the upper Lower Cambrian Bastion and Ella Island formations, north-east Greenland. *Journal of Paleontology* **80:** 1087-1112.

793 **Skovsted CB, Brock GA, Paterson JR, Holmer LE, Budd GE 2008.** The scleritome
794 of *Eccentrotheca* from the Lower Cambrian of South Australia: lophophorate affinities
795 and implications for tommotiid phylogeny. *Geology* **36:** 171-174.
796
797 **Skovsted CB, Holmer LE, Larsson CM, Högström AE, Brock GA, Topper TP,**
798 **Balthasar U, Petterson Stolk, S, Paterson, JR. 2009.** The scleritome of *Paterimitra*:
799 an Early Cambrian stem group brachiopod from South Australia. *Proceedings of the*
800 *Royal Society of London B: Biological Sciences*, rspb-2008
801
802 **Skovsted CB, Brock GA, Topper TP, Paterson JR, Holmer LE. 2011**. Scleritome
803 construction, biofacies, biostratigraphy and systematics of the tommotiid *Eccentrotheca*
804 *helenia* sp. nov. from the early Cambrian of South Australia. *Palaeontology* **54:** 253-
805 286.
806
807 **Skovsted CB, Peel JS. 2011.** *Hyolithellus* in life position from the Lower Cambrian of
808 North Greenland. *Journal of Paleontology* **85:** 37-47.
809
810 **Skovsted C, Betts M, Topper T, Brock GAB 2015.** The early Cambrian tommotiid
811 genus *Dailyatia* from South Australia. *Memoirs of the Association of Australasian*
812 *Palaeontologists* **48:** 1-117.
813
814 **Spencer, LM. 1980.** Paleoecology of a Lower Cambrian Archaeocyathid Interreef
815 Fauna from Southern Labrador. Unpublished MS thesis, State University of New York,
816 Stony Brook, pp.153.
817

Spitzer M, Wildenhain J, Rappsilber J, Tyers M. 2014. BoxPlotR: a web tool for generation of box plots. *Nature methods* **11:** 121-122.

Stanley SM. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca) (Vol. 125). Geological Society of America Memoir Vol. 125.

Stanley SM. 1972. Functional morphology and evolution of byssally attached bivalve mollusks. *Journal of Paleontology* **46:** 165-212.

Stanley SM. 1977. Trends, rates, and patterns of evolution in the Bivalvia. In: Hallam, A ed. *Patterns of evolution, as illustrated by the fossil record.* Amsterdam: Elsevier; 1977. pp. 209-250.

Streng M, Skovsted, CB. 2006. A new mobergellan (small shelly fossils) from the early Middle Cambrian of Morocco and its significance. *Paläontologische Zeitschrift*, **80:** 209-220.

Todt C, Okusu A, Schander C, Schwabe E. 2008. Solenogastres, Caudofoveata and Polyplacophora. In: Ponder WF, Lindberg DR eds. *Phylogeny and Evolution of the Mollusca*, pp. 71-96.

Topper TP, Brock GA, Skovsted CB, Paterson JR 2009. Shelly Fossils from the Lower Cambrian *Pararaia bunyerooensis* Zone, Flinders Ranges, South Australia. *Memoirs of the Association of Australasian Palaeontologists* **37:** 199-246.

Topper TP, Brock GA, Skovsted CB, Paterson JR. 2010. Palaeoscolecid scleritome fragments with *Hadimopanella* plates from the early Cambrian of South Australia. *Geological Magazine* **147:** 86-97.

Topper TP, Brock GA, Skovsted CB, Paterson JR. 2011. *Microdictyon* plates from the lower Cambrian Ajax Limestone of South Australia: Implications for species taxonomy and diversity. *Alcheringa* **35:** 427-443.

Topper TP, Skovsted CB, Peel JS, Harper DA. 2013. Moulting in the lobopodian *Onychodictyon* from the lower Cambrian of Greenland. *Lethaia* **46:** 490-495.

Turton, WH. 1819. A Conchological Dictionary of the British Islands. London pp. 367.

Vannier J, Steiner M, Renvoisé E, Hu SX, Casanova JP. 2007. Early Cambrian origin of modern food webs: evidence from predator arrow worms. *Proceedings of the Royal Society of London B: Biological Sciences* **274:** 627-633.

Vendrasco MJ, Eernisse DJ, Powell II, Fernandez CZ. 2012. Polyplacophora (Mollusca) from the San Diego Formation: a remarkable assemblage of fossil chitons from the Pliocene of Southern California. *Natural History Museum of Los Angeles County Contributions to Science* **520:** 15-72

Vermeij GJ. 1971. Temperature relationships of some tropical Pacific intertidal gastropods. *Marine Biology* **10:** 308-314.

868 **Vermeij GJ. 1973**. Morphological patterns in high-intertidal gastropods: adaptive
869 strategies and their limitations. *Marine Biology* **20:** 319-346.
870
871 **Vermeij GJ. 1976.** Interoceanic differences in vulnerability of shelled prey to crab
872 predation. *Nature* **260:** 135-136.
873
874 **Vermeij GJ. 1977.** The Mesozoic marine revolution: evidence from snails, predators
875 and grazers. *Paleobiology* **3:** 245-258.
876
877 **Vermeij GJ. 1987.** The dispersal barrier in the tropical Pacific: implications for
878 molluscan speciation and extinction. *Evolution* **41:** 1046-1058.
879
880 **Vermeij GJ, Williams ST. 2007.** Predation and the geography of opercular thickness
881 in turbinid gastropods. *Journal of Molluscan Studies* **73:** 67-73.
882
883 **Walcott CD. 1879.** Descriptions of new species of fossils from the Calciferous
884 Formation. *Annual Report of the New York Museum of Natural History* **32**: 129-131.
885
886 **Waller TR. 1981.** Functional morphology and development of veliger larvae of the
887 European oyster, *Ostrea edulis*. *Smithsonian Contributions to Zoology* **328:** 1-70.
888
889 **Williams A, Carlson SJ, Brunton CHC. 2000**. Classification. In: Kaesler RL ed.
890 *Treatise on invertebrate paleontology, vol. H.* Kansas: The Geological Society
891 of America; 2000. pp. 1–29.
892

893 **Williams, A. Holmer, LE. 2002.** Ornamentation and inferred growth, functions and
894 affinities of the sclerites of the problematic *Micrina*. *Palaeontology* **45:** 845-873.
895
896 **Wrona R 1987.** Cambrian microfossil *Hadimopanella* Gedik from glacial erratics in
897 West Antarctica. *Palaeotologia Polonica* **49:** 37-48.
898
899 **Wrona R. 2004.** Cambrian microfossils from glacial erratics of King George Island,
900 Antarctica. *Acta Palaeonlogia Polonica* **49:** 13-56.
901
902 **Yochelson EL. 1958**. Some lower Ordovician monoplacophoran molluscs from
903 Missouri. *Journal of the Washington Academy of Sciences* **48:** 8–14.
904
905 **Zhang XG, & Aldridge RJ. 2007.** Development and diversification of trunk plates of
906 the Lower Cambrian lobopodians. *Palaeontology* **50:** 401-415.
907
908
909 **Figure 1.** Selected taxa investigated in this study. A, *Mobergella holsti* (Moberg, 1892),
910 SMNH X5780, Cambrian of Sweden, scale bar 1 mm. B, *Discinella micans* (Hall,
911 1872), SMNH X5781, Cambrian of North-East Greenland, scale bar 1 mm. C, *Chiton*
912 *tuberculatus* Linnaeus, 1758, SMNH Mo181927, Santa Marta, Colombia. D, *Ostrea*
913 *edulis* Linnaeus, 1758, SMNH 149696, the Netherlands, Yerseke, scale bar 3 cm. E,
914 *Pseudomussium peslutrae* (Linnaeus, 1771), SMNH 57951, Skagerrak Sweden, off
915 Idefjord, Säcken, depth 60-180 m, scale bar 1.5 cm. F, *Tellina lineata* Turton, 1819,
916 SMNH 149793. G, *Lepidonotus squamatus* (Linnaeus, 1758), SMNH 113623, west
917 coast of Sweden, scale bar 1 mm. H, Operculum of *Nerita peloronta* Linnaeus, 1758,

SMNH 149950, Caribbean Sea, Saint Barthelemy. I, *Discinisca lamellosa* (Broderip, 1833), SMNH Br150543, Namibia. J, *Patella* sp., SMNH Mo181928, Western Australia. K, *Tryblidium reticulatum* Lindström 1880, SMNH Mo150432, Silurian of Sweden. All scale bars 1 cm unless otherwise stated. Taxa incorporated in the analysis from published reports are not illustrated here.

Figure 2. *Discinella micans* (Hall, 1872). A, SEM image of *Discinella*, SMNH X5781. B, Schematic example of outlining the total inner surface and the respective muscle scars. Scale bar 1 mm.

Figure 3. Box and beanplot results of the percentage of the inner surface occupied by muscle scars A Boxplot. Center lines show the medians; box limits indicate the 25th and 75th percentiles as determined by R software; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, outliers are represented by dots; crosses represent sample means; bars indicate 95% confidence intervals of the means. Number of specimens of each taxa included in the analysis is provided .Tail and int. refer to the tail valves and intermediate valves of *Callistochiton*. B Beanplot. Black lines show the means; white lines represent individual data points; polygons represent the estimated density of the data.

Figure 4. Co-occuring tubular fragments with *Mobergella holsti* from the Cambrian of Venenäs, Sweden and flat to concave *Discinella micans* specimens from the Cambrian of Labrador, Canada. A, Tubular fragment, SMNH X5784. B-C, Tubular fragment, SMNH X5785. D *Mobergella*, SMNH X5782. E, lateral view of *Discinella*, SMNH

X5783, F, lateral view of *Discinella*, SMNH X5786. G, lateral view of concave *Discinella*, SMNH X5787. All scale bars 1 mm.

Table 1. Table showing distribution, abundance and lithological details of the strata that mobergellan species have been documented from.

SUPPORTING INFORMATION

Table S1. Detailed statistics of the dataset, including mean, median and whisker length and quartile length of investigated taxa.

Table S2. A Results from a one-way ANOVA test. B Pairwise comparison results from a Tukey's Honestly Significant Difference (HSD) test. Tukey's Q below the diagonal, *p*-value above the diagonal. Significant comparisons are in light blue.